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In A Large Northern Idaho Burn:
Effects of Blister Rust and Distance
Along an Elevational Isocline

FINAL REPORT FOR RESEARCH AGREEMENT
#INT-91595-RJVA
University of Colorado at Denver
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FINAL REPORT

Submitted to

USDA FOREST SERVICE INTERMOUNTAIN RESEARCH STATION
FIRE SCIENCES LABORATORY, MISSOULA

For Cooperative Research Project

PATTERNS OF WHITEBARK PINE REGENERATION IN A LARGE NORTHERN IDAHO BURN: EFFECTS OF BLISTER RUST AND DISTANCE ALONG AN ELEVATIONAL ISOCLINE

INT-91595-RJVA

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THE EFFECTS OF BLISTER RUST, AN INTRODUCED DISEASE, ON POST-FIRE REGENERATION OF WHITEBARK PINE: CASE HISTORY--THE SUNDANCE BURN OF NORTHERN IDAHO

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Running head: Blister rust and forest regeneration

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Abstract: In the northern Rocky Mountains, whitebark pine (Pinus albicaulis) is rapidly declining as a result of previous fire suppression practices, outbreaks of mountain pine beetle (Dendroctonus ponderosae), and an introduced disease, whitebark pine blister rust (Cronartium ribicola). Blister rust is potentially the most destructive agent, killing seedlings and the cone-bearing branches of mature trees. We examined densities of whitebark pine regeneration and both the incidence and severity of blister rust infection of seedlings and saplings in the 25 year-old Sundance Burn in the Selkirk Range of northern Idaho, an area heavily impacted by blister rust. We found that the mean regeneration density of whitebark pine was significantly lower than that of two other comparably aged burns. The low density was attributed to the severe damage to the seed source on the burn perimeter, resulting from previous mountain pine beetle infestation and blister rust. Overall, 29% of the whitebark pine regeneration in the Sundance Burn was infected by blister rust. Age and height of regeneration were important predictors of incidence of infection, and height was the most important predictor of severity of infection. Thus, as seedlings grow larger, they present a bigger target to air-borne blister rust spores. With the lack of seed production in the adjacent forest and expected

regeneration mortality, restocking of the Sundance Burn will be a slow process. In blister rust-impacted regions, prescribed fires for managing whitebark pine ecosystems must be restricted to small areas or require artificial restocking with rust-resistance seedlings.

Introduction

Whitebark pine (Pinus albicaulis) populations in the northern Rocky Mountains are decreasing at an alarming rate (Arno 1986; Kendall & Arno 1990; Keane & Arno 1993). The primary causes of the decline are fire suppression, outbreaks of mountain pine beetle (Dendroctonus ponderosae), and white pine blister rust (Cronartium ribicola), an exotic disease. These factors act in synergism in many areas to accelerate losses: Fire suppression results in successional replacement of whitebark pine by shade-tolerant conifers such as subalpine fir (Abies lasiocarpa) and Engelmann spruce (Picea engelmannii), and both rust-infected and senescent whitebark pine trees are more vulnerable to pine beetle infestation (Arno 1986; Keane & Arno 1993). Blister rust is potentially the most damaging factor, both hastening the successional process and killing the cone-bearing branches of whitebark pine and thus reducing the possibilities of future regeneration, even if disturbance occurs.

Whitebark pine is distributed from the Sierra Nevada north through the Cascade Range and the Coast Ranges into southern British Columbia, and from western Wyoming north and west through the Rocky Mountains into southern Alberta and British Columbia (Arno & Hoff 1989). In the northern Rocky Mountains, whitebark pine is successional on favorable subalpine sites and climax on exposed sites, including those

at subalpine elevations, at timberline, and above (Arno and Hoff 1989). Because of its shrubby growth form and inaccessibility, whitebark pine has had limited commercial value. However, ecologically and taxonomically, whitebark pine is of some interest: It is the only New World species of the Cembrae pines, a group characterized by large, wingless seeds, indehiscent cones, and seed dispersal primarily by the nutcrackers (Nucifraga spp.), seed-storing, montane birds of the Corvidae. When whitebark pine cones are available, in late summer and fall Clark's Nutcrackers (Nucifraga columbiana) store shallow subterranean caches consisting of 1 to 15 or more seeds each (mean of about 4 seeds per cache), totalling an estimated 30,000 to 98,000 stored seeds per bird (Tomback 1978, 1982; Hutchins & Lanner 1982). Nutcrackers may carry up to one hundred or more whitebark pine seeds in their throat pouch at any time, flying between parent trees and cache sites (Tomback 1978); they are known to transport whitebark pine seeds as far as 12.5 km (Tomback 1978). Nutcrackers recover these seed stores for food in winter and spring months (Tomback 1978), but in the spring and summer following an abundant cone crop, unretrieved caches may produce clusters of seedlings (Tomback 1982).

Whitebark pine communities are valued for providing watershed protection and wildlife habitat for a number of species, including grouse, elk (Cervus elaphus) and deer (Odocoileus hemionus). The large, nutritious seeds are eaten by

a diverse assemblage of birds and small mammals (Tomback 1978, 1982; Hutchins & Lanner 1982; Halvorson 1986) as well as by black bears (Ursus americanus) and grizzly bears (Ursus arctos) prior to hibernation (Kendall 1983; Mattson et al. 1991). Whitebark pine communities are designated as critical grizzly bear (Ursus arctos) habitat in the areas south of Canada that are still known to have grizzly bears: The Greater Yellowstone Ecosystem, the Northern Continental Divide Ecosystem, the Cabinet-Yaak Ecosystem, and the Selkirk Ecosystem (Peek et al. 1987). In several areas that once supported viable grizzly bear populations (e.g., the Selway-Bitterroot Ecosystem, Selkirk Range, Whitefish Range), whitebark pine populations have been decimated, particularly by blister rust (Kendall & Arno 1990), which may in part account for the decline of grizzlies.

White pine blister rust, a fungal disease of five-needled pines, was first introduced to North America in a shipment of eastern white pine (Pinus strobus) seedlings grown in France that arrived in Vancouver, British Columbia, in 1910. From this entry point, blister rust began infecting western white pine (Pinus monticola) and whitebark pine to the north, south, and east of Vancouver; by 1923 the rust had spread throughout western white pine populations and much of the northern range of whitebark pine (Hoff & Hagle 1990). The disease continues to spread throughout the northern

range of whitebark pine and has appeared in the more arid southern regions (Kendall & Arno 1990).

Bingham (1972) rated whitebark pine as the most blister rust-susceptible of the 14 white pines examined; however, Hoff et al. (1980) gave whitebark pine an average ranking of 7.2 out of 11 (1 being least susceptible), based on genetic mechanisms of resistance. In both studies, western white pine was rated as more resistant than whitebark pine.

In this study we examine whitebark pine regeneration density and both severity and incidence of blister rust infection in the 25 year-old Sundance Burn in the heavily blister rust-infected Selkirk Range of northern Idaho. Two previous studies based on similar methodology examined whitebark pine regeneration about 25 years after fire in western Montana; the study areas were the Sleeping Child Burn in the Sapphire Range and the Saddle Mountain Burn in the Bitterroot Mountains (Tomback et al. 1990; Tomback et al. 1993). Both burns occurred in whitebark pine areas recently surveyed by Keane and Arno (1993) and found to be only lightly infected with blister rust. Thus, they provide data on potential whitebark pine regeneration densities in the near absence of blister rust infection.

Our specific research objectives for the Sundance Burn were:

(1) To determine whether blister rust infection had reduced the density of whitebark pine regeneration in the Sundance

Burn compared to the densities found in the Sleeping Child and Saddle Mountain Burns, which are in areas of lower blister rust incidence.

(2) To examine the severity of blister rust infection in the nearest whitebark pine seed source.

(3) To determine and compare the relative severity and incidence of blister rust in seedling and sapling whitebark and western white pine.

(4) To determine any correlates of incidence or severity of blister rust infection in western white pine and whitebark pine.

Methods

Blister Rust

White pine blister rust is a fungal disease native to Asia and introduced to both Europe and North America. Blister rust requires shrubs of the genus Ribes as an annual, alternate host; the complex life cycle takes four years to complete and involves five different spore forms. In the fall, basidiospores from Ribes spp. infect the needles and occasionally the stems of white pines. The fungus is visible as a needle spot in about 30 days. Inside the needle, the fungus grows towards the stem, resulting in stem infection, i.e., a canker, characterized by yellow-orange swelling, within 12 months (Hoff 1988). In 2 to 3 years, pycniospores are produced on the canker, which secretes nectar; the

nectar attracts insects, which cross-fertilize the canker with pycniospores from other cankers. In 3 years, orange aeciospores are produced by the canker, which then infect Ribes spp., completing the cycle (Hunt 1983).

According to Hunt (1983), once infected, pines may be damaged by blister rust in several ways: (1) death to the part of the tree above a canker, (2) death to the entire branch infected by a canker, or (3) death to the entire tree infected by a basal stem canker, which may result from a branch canker growing into the stem. However, death is usually not directly caused by tissue damage from blister rust, but rather by attacks by other fungus diseases or insects. In addition, mammals and insect larvae may feed on the diseased tissue, causing greater damage.

Blister rust infection may be identified in the field by several signs. The symptom of early infection is a slight swelling in stem or branch tissue; the infection is confirmed by the presence of a yellow-orange patch that is enhanced in color by rubbing with water or by scratching with a knife blade. Older cankers have yellow-orange bark broken by white fruiting bodies (aecia). Indicators of more advanced infection include branches with red-brown foliage or "flags" and the presence of ants, grasshoppers, or aphids, which are attracted to the nectar associated with pycniospores.

Study Area

The Sundance Burn was the result of a lightning-ignited fire in August 1967, that severely burned over 22,600 ha (Anderson 1968) in the Kaniksu National Forest of northern Idaho. About 26 km long and about 8 km wide, the burn runs southwest to northeast; the Selkirk Divide crosses the southern half of the burn. The pre-fire climax forest type was primarily western redcedar (Thuja plicata) and western hemlock (Tsuga heterophylla) (Stickney 1985), with whitebark pine and subalpine fir communities at higher elevations and on more exposed sites.

A study area was selected within the burn based on the following criteria: (1) the unburned whitebark pine seed source must be limited to one end of the burn, (2) there must be available topography at an elevation of 1525 m or above, running perpendicular to the seed source, and (3) the site must be reasonably accessible by four-wheel drive vehicle and hiking. The elevation isocline ensured that the study area remained within suitable whitebark pine habitat, thus reducing the effect of variation in elevation on regeneration densities. We selected an area beginning about 3.5 km east of Sundance Mountain in blocks 10 and 2 on the Mount Casey, Idaho, U.S. Geological Survey quadrangle, and continuing in block 35 on the Mount Roothaan, Idaho, quadrangle (Fig. 1). The study site falls between 48° 27′

30" and 48° 32′ 30" latitude and 116° 40′ 00" and 116° 42′ 30" longitude.

The adjacent unburned whitebark pine seed source is on the east slope of a 1915 m peak at the south end of the study area; fire separated this seed source into a major stand and a minor stand, which was next to our plot transects (Fig. 1). Additional unburned whitebark pine is about 2 km southeast of the study area on Flattop mountain.

Methods

Plot Establishment

We conducted the study from 25 June to 5 July 1992. The first plots, 0A and 0B, were placed on the ridge between the major and minor seed source (1780 m elevation) (Fig. 1). The other plots were established along a northeast-trending transect, which began at the northeastern edge of the minor seed source at points 1A and 1B (1840 m elevation), considered 0 m from the seed source, and extended about 3.4 km into the burn to points 22A and 22B (1845 m elevation) (Fig.1). Twice, the transect was interrupted by a small valley; the first occurred between plots 6 and 7 and the second between plots 9 and 10.

All plots in the study were 50 m long. Beginning at 0 m from the seed source (plots 1A and 1B), two parallel plots (A and B) were established every 150 m along the transect (i.e., 100 m between sequential plots) for a total of 44

plots. In the two cases where valleys were traversed, the distance between sequential plots was greater than 150 m; also, the distance between the plot pair 20 and 21 was 150 m rather than 100 m, because of an intervening area of unsuitable habitat resulting from greater snow accumulation. The "A" plots were established with their 50 m axis along the transect line; the "B" plots were established 10 m due east of the A plots, with their 50 m axis parallel to the axis of the A series.

All plots were initially set up with a width of 2.5 m, but once a 0 density was documented for either whitebark or western white pine, the plot was widened to 5 m and then finally to 10 m to obtain a more realistic assessment of local densities. Density data were standardized to number of regeneration sites (which could be occupied by a single seedling or tree or a cluster, in the case of whitebark pine) per m^2. For each plot, we recorded elevation (based on both topographic maps and altimeter readings), aspect, plot width, and major vegetation. Similar methodology was used in the Sleeping Child and Saddle Mountain studies (Tomback et al. 1990; Tomback et al. 1993).

Regeneration Data

Each whitebark pine and western white pine seedling or sapling was measured for height (cm), or for dbh if taller than 137 cm, and aged by destructive sampling. Rings were

counted in the field under a handlens or in the laboratory later with the aid of a dissecting microscope. For whitebark pine seedling clusters, at least two of the seedlings in a cluster were measured for height and aged. We subjectively assessed regeneration as in good, fair, or poor health.

All whitebark pine and western white pine regeneration was surveyed for blister rust infection according to the methodology developed by R. E. Keane and R. J. Hoff ("Ecodata"). Specifically, this involved counting the number of cankers on tree stems and branches for each individual.

Seed Source Survey

In the major seed source, we surveyed three widely separated plots, each 900 m^2 in area, and examined the density and infection levels of whitebark pine. All snags and live whitebark pine trees were surveyed, measured for dbh, and aged by increment coring. We did not set up plots in the minor seed source but instead examined nearly all living whitebark pine trees there for blister rust and potential cone production.

Statistical Methods

All descriptive statistics and linear regression analyses were performed on an IBM compatible personal computer

using Statgraphics software (version 2.6). We report standard deviations with means. Logistic Regression Analysis, a maximum likelihood technique for non-normally distributed data, was conducted with SAS software on the VAX (mainframe) system.

For whitebark pine seedlings or saplings growing in clusters, the mean age, height, and infection level per cluster were calculated and used in data analysis. This was necessary to meet assumptions of statistical independence. For the remainder of this paper, the term "seedling" will represent both single seedling and sapling regeneration sites and the mean for whitebark pine seedling or sapling clusters, unless otherwise noted.

We used Logistic Regression Analysis to examine the relationship between incidence of infection (dependent variable) and the independent variables age, height, and distance from the whitebark pine seed source (i.e., along the transect from the edge of the burn). Infection was indicated by a binary designation of "1" for infected seedlings and "0" for non-infected seedlings. Species was coded with "0" for western white pine and "1" for whitebark pine. For the Logistic Regression Analysis, the dependent variable, incidence of infection, was transformed into:

$$-\log_{10}(P_{infection}/1-P_{infection}),$$

where $P_{infection}$ is the probability of the seedling being infected (Kleinbaum et al. 1988). Other statistical methods used to test whether the incidence of infection differed significantly among species included the Chi-square test and a Two Sample Test for Proportions.

We defined severity of infection as number of cankers per seedling. In order to examine possible predictive factors for severity of infection, we used Stepwise Regression Analysis with such independent variables as age, height, species, and distance from the seed source. Only infected seedlings were used in this analysis. With the entire sample 1) normality assumptions could not be met, and 2) the large number of non-infected seedlings obscured differences in severity of infection among all the seedlings. We normalized the infection severity data by taking the $\log_{10}$ of number of cankers per seedling to create the dependent variable $\log_{10}$infection (Kleinbaum et al. 1988). Again, in this analysis species was coded as 0 for western white pine and 1 for whitebark pine.

Spearman Rank Correlation Analysis (Siegel 1956) was used to check trends in relationships between variables in the Stepwise Regression analysis. Two Sample t-tests were used to examine whether age and height differed significantly between western white pine and whitebark pine.

Results

Plot Descriptions

The 46 study plots ranged in elevation from 1775 m to 1849 m, with a mean of 1820 m. In general, the plots widened as distance from the seed source increased and as whitebark pine densities decreased; 17 (37%) plots were 2.5 m wide, 23 (50%) were 5 m wide, and 6 (13%) were 10 m wide. The aspect of the plots varied: 21 (46%) northwestern, 9 (20%) northeastern, and 6 (14%) southeastern. Most of the plots were nearly level: the slope per plot ranged from about 0 to 35° with a mean of about 11°. Understory dominants included yarrow milfoil (Achillea millefolium), huckleberry (Vaccinium membranaceum), white rhododendron (Rhododendron albiflorum), beargrass (Xerophyllum tenax), lousewort (Pedicularis contorta), lupine (Lupinus sp.), sedge (Carex sp.), and penstemon (Penstemon sp.). The most common regenerating conifer was subalpine fir. In addition to whitebark pine and western white pine, other regenerating conifers on the plots included Douglas-fir (Pseudotsuga menziesii), Engelmann spruce (Picea engelmannii), lodgepole pine (Pinus contorta), ponderosa pine (Pinus ponderosa), grand fir (Abies grandis), western larch (Larix occidentalis), and western red cedar (Thuja plicata).

Among the plots, live whitebark pine ranged in density from 0 to 0.080 regeneration sites per m^2, with a mean of

0.0077 $\pm$ 0.0131. The mean density of live western white pine was 0.0174 $\pm$ 0.0147 regeneration sites per m^2, more than twice that for whitebark pine (Table 1). However, the mean densities of dead regeneration recorded on the plots were similar for both species.

Of the 58 total whitebark pine regeneration sites, regeneration on 16 sites (27.6%) was in clusters. The number of seedlings per cluster ranged from 2 to 9 with a mean of 4.75 $\pm$ 2.175.

Comparison with Sleeping Child and Sundance Burns

The mean density of whitebark pine regeneration on the study plots in the Sundance Burn 25 years after fire was compared with mean densities obtained for the Sleeping Child and Saddle Mountain burns 26 and 28 years, respectively, after fire. These comparisons indicated that the density of live regeneration in the Sundance Burn was only about one-sixth that of the Saddle Mountain Burn and one-ninth that of the Sleeping Child Burn (Table 2).

Whitebark pine regeneration densities did not differ significantly between the Sleeping Child and Saddle Mountain burns ($\underline{d}$ = 1.704, N.S., $\underline{n_1}$ = 63, $\underline{n_2}$ = 41). However, a comparison among all three burns was significantly different (One-way ANOVA, $\underline{F}$ = 9.773, $\underline{df}$ = 2, 149, $\underline{p}$ = 0.0001).

Blister Rust Infection of Whitebark and Western White Pine

For whitebark pine, four (6.9%) regeneration sites out of the total 58 sites supported dead seedlings; three of the four dead seedlings had symptoms of blister rust. A total of 17 living and dead whitebark pine regeneration sites out of the 58 supported blister rust-infected seedlings, for an overall 0.29 infection frequency. In western white pine, seedlings at three (2%) of the 150 regeneration sites had died and showed signs of blister rust infection. Of the living and dead western white pine, 33 of 150 (or 0.22) regeneration sites were infected by blister rust. The incidence of infection for the combined white pine sample was 0.24. The overall health of non-infected seedlings was rated as "good", whereas the health of infected seedlings was rated as "fair."

For all regeneration sites, the mean number of cankers per whitebark pine seedling was more than double that per western white pine seedling (Table 3). When infected seedlings alone were compared, the mean number of cankers per seedling was again much greater for whitebark pine than for western white pine.

Whitebark and western white pine regeneration was similar in height ($\underline{t} = 0.132$, $\underline{df} = 206$, $\underline{p} = 0.895$) and age ($\underline{t} = -0.2425$, $\underline{df} = 204$, $\underline{p} = 0.809$). For both species, the heights and ages of infected seedlings were greater than that for non-infected seedlings (Table 4). The most severely infect-

ed whitebark pine had 19 cankers. This individual was 115 cm tall, 13 years old, and not a cluster member. Similarly, the most severely infected western white pine had 15 cankers and was 220 cm tall and 14 years of age. Both individuals were at least one standard deviation above the mean age for each species.

For whitebark pine, only four seedlings from clusters were infected. Two of these seedlings belonged to the same three-seedling cluster. The other two were each the only infected cluster members of four-seedling clusters. Thus, of the 16 seedling clusters recorded, three clusters or 18.8% had seedlings infected by blister rust. In contrast, 33% of the single seedling regeneration sites were infected. The numbers of cankers, age, and height were lower for seedlings in clusters than for single seedlings (Table 5).

Factors Predicting Incidence and Severity of Infection

We used several statistical techniques to determine whether seedling age and height, species identity, and distance from the whitebark pine seed source, or some combination of these factors, could predict blister rust infection incidence and severity.

We first examined the incidence of infection with Logistic Regression Analysis. The best model contained age (p = 0.0000), distance (p = 0.0030), and height (p = 0.0632). The likelihood ratio probability for the model was 0.9900:

$$-\log_{10}[P_{infection}/(1-P_{infection})] = 6.3816 - 0.0097*Height - 0.0007*Distance - 0.3862*Age.$$

The second best Logistic Regression model, with a likelihood ratio of 0.9927, included species ($p = 0.0902$), age ($p = 0.0000$), distance ($p = 0.0012$), and height ($p = 0.0465$).

$$-\log_{10}[P_{infection}/(1-P_{infection})] = 6.2593 - 0.0106*Height - 0.00076*Distance - 0.3720*Age + 0.4155*Species.$$

This model suggests that western white pine tends to become infected more readily than whitebark pine.

To further examine the potential influence of species on infection incidence, we performed additional statistical tests. Both indicated that the null hypothesis should not be rejected ($Z = 0.896$, $p = 0.36$; $X^2 = 1.889$, $p = 0.17$, $df = 1$). These results suggest that the best Logistic Regression model should not include species.

We examined the predictive factors for severity of infection (numbers of cankers per seedling) within infected seedlings using Stepwise Regression Analysis. The best model was based only on height (F-ratio = 9.492, $p = 0.034$, $df = 48$) and had an adjusted r^2 of 0.148:

$$Log_{10}Infection = 0.1904 + 0.00699*Height.$$

In an attempt to create a better model, we removed five outliers identified from the above model, but this did not improve the F-ratio or r^2 value. We then included species as a predictor, but this again did not improve the model.

Spearman Rank Correlation Analysis was used to construct a matrix for whitebark pine (Table 6) and for western white pine (Table 7), based on severity of infection (number of cankers), age, height, and distance from the whitebark pine seed source (Table 6 and 7). In both sample groups, height and age were significantly correlated ($p < 0.001$) with infection severity, but distance was not. As expected, height and age were highly correlated with each other in both matrices ($p = 0.0000$).

Status of the Whitebark Pine Seed Source

In the major seed source, the vast majority of the whitebark pine trees were dead, but blister rust infection did not appear to be the primary cause.

The average whitebark pine density for the three plots surveyed, including both live and dead trees, was 0.018 tree sites per m^2, with a range of 0.012 to 0.023. For live trees, the density per plot ranged from 0.008 to 0.010 tree sites per m^2, with a mean of 0.008. The live trees included regeneration under 1 cm dbh (diameter at breast height, or about 1.4 m), which may be degenerate, as well as cone-bearing trees. Two trees of about 35 cm dbh were aged at

206 and 284 years; one had symptoms of blister rust. Most of the dead whitebark pine trees had been weakened or killed by mountain pine beetle infestation before the Sundance fire, as indicated by beetle galleries on snags. A few trees died of unknown causes since the fire.

A survey of almost the entire minor seed source revealed 11 living whitebark pine trees; of these, at least three (27%) showed symptoms of blister rust infection and only 7 trees had produced female cones in 1992.

Discussion

The first objective of this study was to determine if blister rust had significantly reduced whitebark pine regeneration density in the Sundance Burn in comparison to the Sleeping Child and Saddle Mountain burns, which are similar in time elaspsed since fire but are less impacted by blister rust (Keane & Arno 1993). The second objective was to examine the severity of blister rust infection in the whitebark pine seed source. Both are addressed below.

We found that the regeneration density for whitebark pine in the Sundance Burn was significantly lower than in the other two burns. However, at present time the lower density of regeneration cannot be attributed to mortality caused by blister rust. Although about 29% of the whitebark pine

regeneration was infected with blister rust, we found only 4 dead seedlings--three with symptoms of blister rust.

The most obvious explanation for the lower regeneration density is the low density of live, cone-bearing trees in the major, unburned seed source. Widespread loss of whitebark pine occurred before the fire as a result of infestation by mountain pine beetles. In addition, among those cone-bearing trees that survived, the incidence of blister rust is reasonably high. We presume that the results of our survey represent the general condition of unburned whitebark pine communities along the perimeter of the burn. The low seed production in this forest area is not likely to result in large numbers of nutcrackers storing seeds in adjacent terrain.

A comparison of unburned seed sources among all three burns indicates that the overall (live and dead) mean density of whitebark pine in the Sundance Burn seed source was somewhat lower than that found in the other two study areas. The mean whitebark pine seed source densities for the Sleeping Child and Saddle Mountain burns (n = 2 plots each) were 0.064 and 0.114 tree sites per m^2, respectively (D. F. Tomback, L. A. Hoffmann, and S. K. Sund, unpublished data). It is conceivable that even in the absence of mountain pine beetles and blister rust, the rate of regeneration in the Sundance Burn would be somewhat lower than that observed for the other two burns.

Although blister rust to date has not resulted in a high incidence of regeneration mortality in the Sundance Burn, it has had an impact on the health of many of the trees. Also, once seedlings develop cankers, the majority may live less than three more years (Hoff & Hagle 1990). In the Sundance Burn, this means that 29% of all regeneration will be dead by 1995, with uninfected seedlings also becoming infected.

The third objective of the study was to compare the incidence and severity of infection in western white and whitebark pine. In the Sundance Burn, the incidence of blister rust infection in western white pine was less (0.22) but not significantly different than that for whitebark pine (0.22). Previous studies suggest that whitebark pine is, however, less resistant to blister rust than western white pine (Bedwell & Childs 1943; Childs & Bedwell 1948; Bingham 1972; Hoff et al. 1972; Hoff & Hagle 1990). Examining only the regeneration that was infected by blister rust, we found that, in fact, whitebark pine seedlings had on average nearly double the number of cankers compared to western white pine.

We were successful in achieving the fourth objective: identifying the factors that might predict both incidence and severity of blister rust infection in both pines. Results of the logistic regression analysis indicated that distance from the whitebark pine seed source, age, and height of seedlings were important predictors of incidence

of infection. Both age and height were highly correlated. As seedlings grow, they are more likely to become infected with blister rust. For both western white pine and whitebark pine, the ages and heights of infected seedlings were greater than those for non-infected seedlings. Through time, the seedling becomes a larger target. In fact, as the present regeneration in the Sundance Burn grows, seedlings may become infected at an accelerated rate.

It is not readily apparent how distance from the whitebark pine seed source relates to the infection incidence for both pines. One explanation is that air-borne spores are impeded by the forest, which also had living Engelmann spruce and subalpine fir. Another possibility is that the location of concentrations of Ribes with respect to the prevailing winds increased infection incidence towards the north.

The best Stepwise Regression model included seedling height as the only predictor of infection severity. This suggests that as seedlings grow, the increased surface area leads to acquisition of additional cankers. The addition of species as a variable did not improve the model, despite the fact that whitebark pine may be more vulnerable to infection. Height and age were both significantly correlated with infection severity in a Spearman Rank Correlation matrix, but distance from the seed source was not.

Whitebark pine seedlings in clusters had both lower incidence of blister rust infection and lower severity of infec-

tion (fewer cankers per seedling) than did solitary whitebark pine seedlings. However, the seedlings in clusters were shorter and younger than the solitary seedlings, which may explain these differences in susceptibility. It is possible that within-cluster mortality over time reduces the occurrence of clusters among the older regeneration.

Overall, the results of this study suggest that with both the whitebark pine seed source so damaged and the prevalence of white pine blister rust in this region, regeneration of whitebark pine to pre-burn densities in the Sundance Burn may be a slow process. Mean living whitebark pine regeneration density currently in the burn (0.0077 regeneration sites per m^2) is about two-thirds the mean overall density (living plus dead trees) of whitebark pine trees more than 1 cm dbh recorded in the major seed source. However, future mortality caused by blister rust and other factors will greatly delay restocking.

On a more optimistic note, it is likely that much of the whitebark pine regeneration that survives to maturity in the Sundance Burn will carry genes for one or more of the resistance mechanisms that thwart white pine blister rust infection (Hoff et al. 1980; Hoff & Hagle 1990). Burns and clearcuts may, in fact, facilitate the establishment of rust-resistant populations (Hoff, unpublished data). However, only after resistance is widespread will seral and climax whitebark pine communities in blister rust regions

regenerate reliably and in a natural timeframe. Until then, the use of prescribed fire for managing whitebark pine ecosystems must be restricted to small areas or require artificial restocking with rust-resistant seedlings.

Acknowledgments

We are grateful to the USDA Forest Service Intermountain Research Station, Ogden, Utah, for funding this study. Accommodations and laboratory facilities during fieldwork were provided by the Priest River Experimental Forest; we gratefully acknowledge Robert Denner, manager of the forest, for logistic support and helpful information. We also thank Mark Flower and Mary Powell for their help in the field.

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Table 1. Regeneration densities (regeneration sites per m^2*) for whitebark pine and western white pine in the Sundance Burn. Infected seedlings have symptoms of white pine blister rust.

	Regeneration density (sites per m^2)		
Pine species	Mean	S. D.	Range
Whitebark pine			
living	0.0077	0.0131	0 - 0.0800
dead	0.0004	0.0024	0 - 0.0160
infected	0.0024	0.0056	0 - 0.0240
Western white pine			
living	0.0174	0.0147	0 - 0.0560
dead	0.0003	0.0014	0 - 0.0080
infected	0.0040	0.0060	0 - 0.0320

* For whitebark pine, a regeneration site supports either a cluster of seedlings or a single seedling; for western white pine, a regeneration site supports a single seedling.

Table 2. Comparison of whitebark pine regeneration density in the Sundance Burn with regeneration density in the Sleeping Child and Saddle Mountain burns.

Burn study area	Burn year	Study year	Regeneration density (sites per m^2)		
			Mean density	S. D.	Range
Sundance	1967	1992	0.0081	0.0077	0 - 0.0800
Sleeping Child	1961	1987	0.0700	0.1040	0 - 0.5120
Saddle Mountain	1960	1988	0.0440	0.0510	0 - 0.1600

Table 3. Comparison of blister rust infection severity (number of cankers per seedling) between whitebark pine and western white pine.

Pine species	Number of cankers per seedling		
	Mean	S. D.	Range
All seedlings			
Whitebark pine	1.4	3.8	0 - 19
Western white pine	0.6	1.6	0 - 14
Infected seedlings			
Whitebark pine	4.9	5.7	1 - 19
Western white pine	2.7	2.4	1 - 14

Table 4. Mean ages and heights of infected and non-infected regeneration and both combined for whitebark and western white pine.

Pine regeneration	Age (yr)			Height (cm)		
	Mean	S. D.	Range	Mean	S. D.	Range
Infected						
Whitebark	12.0	4.2	3 - 20	77.7	40.8	13.8 - 172
Western white	11.2	3.2	2 - 20	97.3	57.2	30.0 - 220
Non-infected						
Whitebark	6.7	3.4	3 - 14	41.3	48.5	4.0 - 167
Western white	7.5	2.8	2 - 13	40.4	36.9	2.5 - 206
Combined						
Whitebark	8.3	4.4	3 - 20	51.9	49.0	4.0 - 172
Western white	8.1	3.2	2 - 20	52.9	48.2	2.5 - 220

Table 5. Comparison of ages, heights, and overall number of cankers per seedling or sapling between whitebark pine regeneration in clusters and solitary.

No. of regeneration sites	Age (yr)			Height (cm)			No. of cankers per seedling		
	$\bar{x}$	S. D.	Range	$\bar{x}$	S. D.	Range	$\bar{x}$	S. D.	Range
Clusters									
16	6.2	4.0	3 - 18	22.4	22.4	5.3 - 87.0	0.14	0.43	0 - 2
Solitary									
42	9.1	4.3	3 - 20	63.2	51.7	4.0 - 172	1.93	4.32	0 - 19

Table 6. Spearman Rank Correlation matrix for whitebark pine, including the variables infection severity (number of cankers per seedling), regeneration height (cm) and age (yr), and distance (m) from the whitebark pine seed source. The top number is r_s and the bottom number is the probability with df = 56.

	Infection severity	Height	Age	Distance
Infection severity	-------	0.4805	0.5119	0.1443
	-------	0.0004	0.0001	0.2845
Height		-------	0.8193	-0.3038
		-------	0.0000	0.0243
Age			-------	-0.1808
			-------	0.1799
Distance				-------

Table 7. Spearman Rank Correlation matrix for western white pine, including the variables infection severity (number of cankers per seedling), regeneration height (cm) and age (yr), and distance (m) from the whitebark pine seed source. The top number is r_s and the and the bottom number is probability with df = 150.

	Infection severity	Height	Age	Distance
Infection severity	-------	0.4922	0.4983	0.0743
	-------	0.0000	0.0000	0.3645
Height		-------	0.8102	-0.0309
		-------	0.0000	0.7062
Age			-------	-0.0053
			-------	0.9484
Distance				-------

Legend

Figure 1. Map of study area within the Sundance Burn, Kaniksu National Forest, Selkirk Range, northern Idaho. Path of 3.5 km transect heading northeast from southern burn boundary is indicated; discontinuities between plot pairs 6A-6B and 7A-7B and 9A-9B and 10A and 10B are valleys crossing the transect ridgeline. Inset shows location of Mount Roothaan and Mount Casey U.S.G.S. quadrangles in Idaho.

Fig. 1

Study Area Map: Blocks 10 and 2 on Mount Casy, Idaho, U.S.G.S. quadrangle and Block 35 on the Mount Roothaan, Idaho, U.S.G.S. quadrangle.